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THE OCCURRENCE OF BUFF AND GRAY PELAGE IN WIDELY SEPARATED GEOGRAPHIC RACES OF THE DEER-MOUSE (*PEROMYSCUS MANICULATUS*)

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INTRODUCTION

THE rate of evolution of animals in nature can be estimated accurately only when it becomes possible to express the variations of wild populations in terms of variations in gene frequencies. Such pioneer efforts as those of Sumner (1932) and Dice (1940) have convincingly demonstrated the enormous range of variability in natural populations of *Peromyscus*. Further progress toward an understanding of the causes for physical differences between local populations, however, requires a different approach. The mode of inheritance of characters that distinguish natural populations must be analyzed, and the genotypes of wild-living individuals must be determined. It is, in a sense, unfortunate that our knowledge of the so-called mutant characters, of little or obscure importance to the immediate survival of the animal in nature, far exceeds our information about characters that receive general expression in natural populations. A beginning has been made, however, toward an understanding of the genetic basis for these "wild-type" characters.

Recent studies of color variation in the deer-mouse of the subspecies *Peromyscus maniculatus blandus* have shown that the buff and gray color phases of this race are produced by Mendelian alleles (Dice, 1933; Blair, 1947*a*). Populations of this subspecies of deer-mouse in the Tularosa Basin, New Mexico, have been sampled, and the frequencies of the two alleles in local populations of that area have been estimated (Blair, 1947*b*).

The present report deals with the results of experiments designed to test for the occurrence of these color genes in other populations from distant parts of the range of *Peromyscus maniculatus*. It includes also an attempt to classify as buff or as gray the field-caught specimens of this species in the collection of the Laboratory of Vertebrate Biology.

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METHODS

All of the deer-mice discussed herein were kept under standard conditions in the Laboratory of Vertebrate Biology at Ann Arbor, and all were fed a standard ration. The hybrids produced in the crosses between the several strains of mice were raised to an age of five or more months, when they were prepared as flat skins. The shade of pelage of some of these hybrids has been measured with a Photovolt reflection meter, using a standard technique (Blair, 1947*a*). Classification into color types was made after the mice had been prepared as specimens.

The field-caught mice that were examined for the buff and gray characters were brought into the laboratory in past years to initiate stocks for variability studies. They have been prepared as flat skins and stored in museum cases. These mice represent random samples of the populations from which they were taken.

STRAINS OF DEER-MICE

Representatives of five strains of deer-mice, either field-caught mice or their direct descendants, have been used in the crosses with selected color strains of *blandus*. The origin of the stocks used is as follows:

Blandus, Tularosa. These color strains of *blandus* have been described in detail elsewhere (Blair, 1947*a*). Most of the *blandus* mice used in the crosses were homozygous for recessive gray (genotype $g\,g$). Most of these grays were also homozygous for another, dominant gene, black-tipped (genotype $B\,B$), but, as will be indicated in the text, a few heterozygotes ($B\,b$) and a few mice that were homozygous for recessive brown-tipped ($b\,b$) were also used. Black-tipped buffs ($BB\;GG$) were crossed with two of the stocks from other localities.

Nebrascensis, Meade. This stock originated from six females and seven males trapped by C. W. Hibbard about fourteen miles southwest of Meade, Meade County, Kansas. The field-caught mice were received in the laboratory on August 22, 1939.

Gracilis, Pine Lake. These mice descended from eight males and eight females that were trapped by W. F. Blair near Pine Lake, Alger County, Michigan. The field-caught mice reached the laboratory on September 24, 1940.

Nubiterrae, Mountain Lake. Fourteen males and five females were collected by J. S. Rogers, Jr., near Mountain Lake, Virginia. They were received on July 22, 1939.

Oreas, Oyster Bay. This stock originated from nine males and six females that were taken by H. J. Leraas on Oyster Bay, about ten miles west of Olympia, Washington. The field-caught mice were received in the laboratory on December 13, 1940.

Oreas, Silver Lake. Nine males and two females were trapped, July 18 and 19, 1940, by Lee R. Dice about five miles west of Eatonville, Pierce County, Washington.

CROSSES BETWEEN *blandus* COLOR TYPES AND OTHER GEOGRAPHICALLY DISTANT RACES

Crosses were made between certain of the *blandus* color strains and deer-mice from the five distant localities described above. These mice from other localities are fairly representative of the species *maniculatus.* Two stocks are from the Pacific Northwest. One is from the southern range of the species in the Eastern forest. One is from the northern part of the range in the Eastern forest. Another is from the central Great Plains.

The crosses were made to test the hypotheses that (1) the buff character of other races of deer-mice results from the same major gene that produces buff *blandus,* and that (2) all gray deer-mice have the recessive gene for gray in common. The results of the crosses are summarized in Tables I and II. The segregation of color characters in the crosses is discussed below.

Gray *blandus* × Buff *nebrascensis*

The *nebrascensis* deer-mice, from southwestern Kansas, are a rich buff in pelage. Ten field-caught mice have been examined, and all are buff, although there is some variation in the saturation of yellow-orange pigment. Two of these buff *nebrascensis* were crossed with gray *blandus.* The two matings produced seventeen F_1 mice, all of which were buff. This indicates that the buff of the *nebrascensis* dominates the *blandus* gray. Although all F_1 mice were buff, there was much variation in shade and saturation of color. One of the matings, between a bright buff *nebrascensis* and a gray *blandus,* produced five bright buff offspring. The other mating, between a dull buff *nebrascensis* and a gray *blandus,* produced a variable lot of twelve dull buff mice.

Four pairs of the F_1 mice produced an F_2 generation of sixty-six buffs and twenty-seven grays (Table I). The ratio of buffs to grays does not depart significantly from the expected three to one ratio for a simple Mendelian cross. The gray segregants were pale and did not differ in appearance from pale gray *blandus.* This is taken to indicate that the *nebrascensis* mice contributed no appreciable quantity of modifiers of gray to the cross. The buff segregants were variable in the shade and saturation of color. Each sibship contained some bright buff mice and some mice which, presumably due to the segregation of minor modifying genes, were of variable shades and saturations of buff.

Seven of the F_1 mice, mated back to gray *blandus,* produced a backcross generation of forty-four buff and thirty-seven gray mice (Table II). The buff–gray ratio does not differ significantly from the expected one to one ratio for a simple backcross. The grays were pale in shade and similar to gray *blandus* in appearance. The buffs, like the F_2 buffs, were variable in shade and saturation of color. One sibship contained one brown-tipped buff and one brown-tipped gray. The brown-tipped presumably came from the *blandus.* The brown-tipped mice were of medium shade and were similar in appearance to *blandus* mice of corresponding phenotype.

TABLE I

SEGREGATION OF BUFF AND GRAY PHENOTYPES IN CROSSES BETWEEN *blandus,* TULAROSA, NEW MEXICO, COLOR STRAINS AND DEER-MICE FROM OTHER, DISTANT LOCALITIES

Crosses	F_1			F_2			
	Expected Number	Phenotype	Observed Number	Expected Number	Classes of Phenotypes	Observed Number	χ^2
Gray *blandus* × buff *nebrascensis*—Meade	17	Buff	17	69.75	Buff	66	0.806
				23.25	Gray	27	
Buff *blandus* × buff *nebrascensis*—Meade	17	Buff	17	41.00	Buff	41	....
Gray *blandus* × buff *gracilis*—Pine Lake	7	Buff	7	2.25	Buff	2	....
				0.75	Gray	1	
Buff *blandus* × buff *gracilis*—Pine Lake	8	Buff	8	....	....	......	....
Gray *blandus* × buff *nubiterrae*—Mt. Lake	51	Buff	44	6.00	Buff	4	....
		Gray	7	2.00	Gray	4	
Gray *blandus* × gray *nubiterrae*—Mt. Lake	9	Gray	9	8.00	Gray	8	....
Gray *blandus* × buff *oreas*—Oyster Bay	6	Buff	6	10.50	Buff	10	....
				3.50	Gray	4	
Gray *blandus* × buff *oreas*—Silver Lake	8	Buff	8	13.50	Buff	13	....
				4.50	Gray	5	

The dominance of the *nebrascensis* buff over the *blandus* gray in the F_1 and the segregation in the F_2 and backcross generations indicates that these are allelic genes and that the buff dominates the gray. The similarity in appearance between the *nebrascensis* buff and the *blandus* buff, and the results of the cross to be described below, indicate that the same major gene for buff pelage is common to the *blandus* buffs and the *nebrascensis* buffs, at least to those from the Meade locality.

Buff *blandus* × Buff *nebrascensis*

Two of the buff *nebrascensis* were crossed with black-tipped buff *blandus*. One mating produced six and the other produced eleven buff offspring. Five members of one sibship, which were prepared as specimens, had an intense saturation of yellow-orange, but they varied among themselves considerably in shade of pelage. Four pairs of these F_1 mice were mated and produced an F_2 generation of forty-one buff mice (Table I). These mice showed the same sort of variability in shade and saturation of pelage color, presumably due to the segregation of minor modifying genes, that was present in the buffs of the F_2 and backcross generations of the cross between gray *blandus* and buff *nebrascensis*. There was no other evident segregation. It seems evident, then, that the *blandus* and *nebrascensis* buffs are produced by the same dominant gene for buff pelage.

Gray *blandus* × Buff *gracilis*

The *gracilis* stock, from the Upper Peninsula of Michigan, descended from seventeen dark buff, field-caught mice. Two of the buff *gracilis*, crossed with gray *blandus*, produced seven moderately bright buffs in the F_1 generation. A mating between two of the F_1 mice resulted in an F_2 generation of

TABLE II

SEGREGATION OF COLOR PHENOTYPE IN BACKCROSSES OF HYBRIDS (BETWEEN *blandus*-GRAY AND BUFF DEER-MICE FROM OTHER LOCALITIES) TO *blandus*-GRAY

Backcrosses	Expected Number	Classes of Phenotypes	Observed Number	χ^2
F_1 (gray *blandus* × buff *nebrascensis*) × gray *blandus*	40.50	Buff	44	0.605
	40.50	Gray	37	
F_1 (gray *blandus* × buff *gracilis*) × gray *blandus*	35.00	Buff	30	1.429
	35.00	Gray	40	
F_1 (gray *blandus* × buff *nubiterrae*) × gray *blandus*	14.00	Buff	16	0.571
	14.00	Gray	12	
F_1 (gray *blandus* × buff *oreas*—Oyster Bay) × gray *blandus*	37.50	Buff	42	1.080
	37.50	Gray	33	
F_1 (gray *blandus* × buff *oreas*—Silver Lake) × gray *blandus*	40.00	Buff	38	0.200
	40.00	Gray	42	

one gray and two buff mice (Table I). The gray was no different from that of gray *blandus* mice. One buff was moderately bright; the other was dull in appearance and had a low intensity of yellow-orange pigment.

Four of the F_1 mice were backcrossed to gray *blandus* and produced thirty buff and forty gray offspring (Table II). The ratio of buffs to grays does not depart significantly from the expected one to one ratio for a simple backcross. The grays did not differ in appearance from gray *blandus* mice. The buffs were highly variable. Some were bright, with a high intensity of yellow-orange; others were dull, with a low intensity of yellow-orange.

The gray *blandus* used in one of the original and backcross matings was in the brown-tipped phase. The backcross generation, in this case, contained six black-tipped buffs, six black-tipped grays, six brown-tipped buffs, and three brown-tipped grays. The brown-tipped buffs and grays resembled corresponding phenotypes, of average shade, in *blandus*. The results of the crosses between *blandus* and *gracilis* indicate that the buff of *gracilis* is an allele of the gray of *blandus*. The similarity of the hybrid buffs, in both the black-tipped and brown-tipped phases, to corresponding *blandus* types strongly suggests that the *blandus* buff and the *gracilis* buff are both produced by the same major color gene. The buff of both subspecies dominates gray, which furnishes additional cause to believe that the buff of both results from the same gene.

Buff *blandus* × Buff *gracilis*

Three of the buff *gracilis* crossed with buff *blandus* produced an F_1 generation of eight buffs. The hybrids were extremely variable in their saturation of yellow-orange pigment. One sibship contained only one mouse, which was dull buff and had a medium saturation of yellow-orange. Another sibship had one bright buff, one of medium brightness, and one dull buff that had a low saturation of yellow-orange. The variability of the buff hybrids presumably comes from various combinations of several minor modifying genes that affect the intensity of the yellow-orange pigment.

Gray *blandus* × Buff *oreas*—Oyster Bay

Four field-caught *oreas* from Puget Sound, Washington, are dark in shade and buffy in tone. The yellow-orange pigment in these mice is of medium or low intensity. One of the buff *oreas* mice was crossed with a gray *blandus*, and the mating produced six dull buff offspring. There was little variability in shade of pelage or in amount of yellow-orange saturation in this family of six hybrids. Two mated pairs of the F_1 mice produced an F_2 generation of ten buffs and four grays. The buff–gray ratio is close to the expected three to one ratio (Table I). The grays resembled dark gray *blandus*. The buffs in both families of F_2 hybrids were extremely variable, which presumably indicates numerous minor modifiers of buff in the *oreas*. Each family had at least one fairly bright buff and also intermediates between bright buff and dull buff. Two mice of one family were a "chocolate" buff in appearance, and one mouse of the other family was of this type.

Four of the F_1 hybrids were backcrossed to gray *blandus.* The backcross generation comprised forty-two buffs and thirty-three grays, which is within the limits of variability for the expected one to one ratio (Table II). The gray *blandus* used in the original cross and for the backcross were heterozygous for brown-tipped; thus, the segregation in three sibships of the backcross generation was into four classes. The black-tipped and brown-tipped grays resembled corresponding phases of gray *blandus.* The black-tipped buffs were less variable than the F_2 buffs and were low in yellow-orange saturation. The buff of *oreas,* like the buff in the other races, appears to result from the same gene that produces the buff *blandus.* The differences in appearance of the two buffs apparently are caused by several modifying genes.

Gray *blandus* × Buff *oreas*—Silver Lake

The eleven field-caught *oreas* from Silver Lake, Washington, resembled the *oreas* from Oyster Bay. One Silver Lake *oreas* was crossed with a gray *blandus.* Eight buff offspring resulted from this cross. These buffs were variable in shade of pelage and ranged from moderate to low in saturation of yellow-orange. An F_2 generation, from four pairs of the hybrids, comprised thirteen buffs and five grays. The buff–gray ratio is within the limits of probability for the three to one ratio that would be expected if this buff is a single unit dominant over *blandus* gray. The grays, two of which were in the brown-tipped phase, resembled corresponding phases of dark gray *blandus.* The buffs were variable. Two had moderate intensities of yellow-orange pigment; the others were low in intensity of this pigment. There was much variation in general shade of pelage.

Seven of the F_1 hybrids were backcrossed to gray *blandus.* Their progeny comprised thirty-eight buffs and forty grays. The proportions of buffs and grays are close to the expected one to one ratio (Table II). The grays resembled gray *blandus.* The buffs varied in shade and in saturation of yellow-orange pigment. One sibship contained three buffs in the brown-tipped phase. Two of these resembled brown-tipped buff *blandus.* The other one was, presumably from the action of modifying genes, more dull and more brown than the corresponding type of *blandus.* The buff of this *oreas* stock, like that of the *oreas* from Oyster Bay, therefore, appears to be produced by the same major gene that produces buff *blandus.*

Gray *blandus* × Buff *nubiterrae*

Fourteen of seventeen field-caught *nubiterrae* from Mountain Lake, Virginia, were fairly bright buff in appearance. Six apparently buff offspring of the field-caught mice were crossed with gray *blandus.* Three of the ensuing sibships contained an aggregate of twenty-four variable buffs. One was very bright buff, four were moderately bright buff, and nineteen were a dull "chocolate" buff similar to the "chocolate" buffs among the Oyster Bay *oreas* hybrids. Three sibships comprised twenty-one buffs, which showed the same type of variability as was present in the families mentioned above, and five apparent grays. These suspected grays were more brown in appearance than gray *blandus.*

Two pairs of buff hybrids produced an F_2 generation of four variable, but relatively bright, buffs and four variable grays. One of the grays resembled dark gray *blandus;* the others were more chocolate-brown in appearance than were the gray *blandus* mice.

Five of the buff F_1 mice were backcrossed to gray *blandus.* The backcross generation comprised sixteen variable buffs and twelve grays. The buff–gray ratio does not depart significantly from the expected one to one ratio. The gray segregants in this cross, unlike those in the crosses involving other stocks, differed from gray *blandus.* These hybrid grays were all more brown in appearance than were the gray *blandus* mice. It appears that the *nubiterrae* mice possessed certain modifiers of gray that were not observed in the crosses involving other stocks. The evidence from this cross suggests that the doubtful grays that segregated out in the F_1 generation of the cross were grays. Like the grays in this generation, they were more brown in appearance than were the gray *blandus.*

Gray *blandus* × Gray *nubiterrae*

Three of the seventeen field-caught *nubiterrae* were darker in shade and more gray in appearance than the others. These three mice were thought to be possibly gray rather than buff, although they had low intensities of what appeared to be yellow-orange pigment. One of these mice was mated to a gray *blandus.* The nine offspring of this mating were gray. One resembled dark gray *blandus,* and the others were slightly more brown than *blandus.* Two of these brownish gray hybrids, when mated together, produced an F_2 generation of eight grays. Three of the grays resembled dark gray *blandus,* and the others were more brown than the *blandus* mice were.

The modification in tone of the *blandus* gray, when crossed with *nubiterrae,* evidently results from the action of one or more modifying genes. This effect is quite different from the intensification of the shade of gray that is obtained when pale gray *blandus* are crossed with other deer-mice that have a dark shade of pelage. If I am correct in believing that the gray of *nubiterrae* and of *blandus* is produced by the same major gene, with different modifiers, then the *nubiterrae* stock comes from a population having a mixture of buff and gray genes.

BUFF AND GRAY PHASES IN SAMPLES OF WILD POPULATIONS

All field-caught specimens of *Peromyscus maniculatus* in the collection of the Laboratory of Vertebrate Biology have been examined for the buff–gray pelage characters. These specimens total 2467 and represent eighteen named races of deer-mice from 173 localities in North America. Four regions, the Great Lakes states, northern plains, northwestern United States, and the southwestern deserts, are most heavily represented. Some specimens are available, however, from most parts of the range of the species in the United States.

Not all of the mice can be classified positively as buffs or grays. Modifiers of gray, such as were present in the *nubiterrae* stock that was crossed with gray *blandus,* are apparently widespread in the species. The buffs are extremely variable in their intensity of yellow-orange pigment and in their shade of pelage. Certain intensifiers of shade of pelage often suppress buffiness in mice that are genotypically buff (Blair, 1947*a*). It is not possible, therefore, to classify all deer-mice in respect to buff and gray without breeding tests.

Of the 2467 specimens examined, 2089 are classified as buff. These come from 172 localities and represent eighteen subspecies. Many of these buffs are more brown, or chocolate, in appearance than is buff *blandus.* Grays of the *blandus* type total 177, but 158 of these are from the Tularosa Basin, New Mexico. Two other stocks of *blandus,* from the Davis Mountains of Texas, contain grays of this type. One of three specimens of *rufinus* from Highrolls in the Sacramento Mountains, New Mexico, resembles the gray *blandus.* Two of twenty-three *artemisiae* from Troy, Idaho, resemble gray *blandus.* One of 139 *maniculatus* from Isle Royale in Lake Superior is indistinguishable from dark gray *blandus.*

Seventy-five of the mice examined are possibly gray. They are more brown in appearance than are gray *blandus* mice, and like the *nubiterrae* grays used in the *blandus–nubiterrae* cross, they appear to have low intensities of yellow-orange pigment. Breeding tests would be required to determine whether such mice were buff or gray. Such a test did indicate that the *nubiterrae* mice of this type are modified grays rather than buffs. These presumed grays were mostly in samples from populations with dark shades of pelage. Stocks of *hollisteri, rubidus,* and *artemisiae* from the forests of the Northwest and of *maniculatus* and *nubiterrae* from the Eastern forests contained mice of this type. Other specimens of this possible gray were found in the dark-colored race *bairdii* of the prairies and in *osgoodi* and *gambeli.* It is noteworthy that two of the stocks in which grays resembling gray *blandus* were present contained many of these other, supposed grays. The stock of *artemisiae* from Troy, Idaho, in addition to two grays of *blandus* type, contained nine of this other type and twelve buffs. The stock of *maniculatus* from Isle Royale, Michigan, in addition to one *blandus*-type gray, contained thirty-two mice that were classified as the modified gray and 106 that were classified as buffs or possible buffs.

There are 117 specimens that, while low in intensity of yellow-orange pigment, appear to be probably buff rather than gray. These mice could be classified with certainty only by a breeding test.

Some generalizations may be made from the examination of the field-caught specimens even though it is impossible to classify all individuals in respect to color type. It is very evident that most deer-mice are buff.

Gray deer-mice most frequently inhabit the Southwestern deserts, but some grays do occur in other distant populations. Grays that resemble gray *blandus* rarely are present in these other populations. Brownish gray mice that possibly are modifications of the gray observed in *blandus,* presumably through the effects of other genes, occur in several widely separated populations of the species.

Deer-mice of the subspecies *nebrascensis* from the Nebraska sandhills have a type of dichromatism. An aggregate of 166 specimens from eighteen localities in and near the sandhills was examined, and all of the mice appear to be of the buff phase. Of these, 124 mice are a clear, rich yellow-orange in appearance, and forty-two are relatively dull in appearance and dark in shade of pelage. Clark (1938) crossed some of these clear buff *nebrascensis* with dark-colored mice of the subspecies *bairdii* and *rubidus,* which he called gray. From these crosses he obtained evidence that the *nebrascensis* character is dominant over the dark shade of pelage of *bairdii* and *oreas.* His material has been examined by me, and it is evident that the characters he was dealing with do not correspond to the buff and gray of *blandus,* for all of his mice are buffs by my classification. The relating of these characters to other described color characters of the deer-mouse must await further investigation.

DISCUSSION

The cross matings showed that the gray of *blandus* is recessive to the buff of (1) *nebrascensis* from southwestern Kansas, (2) *gracilis* from northern Michigan, (3) *nubiterrae* from Virginia, and (4) two stocks of *oreas* from the state of Washington. The resemblance of buff *blandus* to the buff segregants in the crosses and the lack of evident segregation in the F_2 of the cross between buff *blandus* and buff *nebrascensis* indicate that the buff of the other races of *maniculatus* is probably produced by the same major gene that produces buff *blandus.*

The *nubiterrae* stock was the only one of the five stocks tested that had both of the buff–gray alleles. Failure to find the recessive gray gene in the other races is no indication that these races lack the gene. Too few individuals were tested for any conclusions about the frequencies of the two genes to be drawn from these data. Actually, gray mice resembling gray *blandus* were observed in samples from three other subspecies, and brownish gray mice, presumably produced by the gene for gray and other, modifying genes, were among field-caught specimens from eight geographic races.

The buff segregants in the crosses between the *blandus* color strains and the other races are extremely variable. Some are bright buff in appearance; others are dull buff. The buffs vary extremely in the intensity of the yellow-orange pigment in the agouti band of the body hairs. The wide range of variation in the hybrid buffs is taken to indicate numerous modifying genes with minor effects on the buff phenotype. Similar effects of these minor genes have been observed in crosses between color strains of *blandus* (Blair, 1947*a*). The buff field-caught specimens examined from many parts of the species range vary similarly. The variability is so great that, lacking the opportunity for breeding tests, not all of these field-caught mice can be definitely classified as buffs.

The gray segregants in the crosses between gray *blandus* and the *oreas, gracilis,* and *nebrascensis* show very little variation. The hybrid grays resemble gray *blandus* of corresponding shades of pelage. The *blandus* gray is darkened by the cross to the relatively dark races of deer-mice, just as it can be darkened by crossing a pale with a dark gray *blandus*. The cross with *oreas,* which, in shade of pelage, is the darkest of the races studied, produces the darkest shade of grays (Table III). The grays in the backcross generation of the crosses are paler than those of the F_2 generation. The minor modifiers of the intensity of shade are presumably reduced in number by the backcross to gray *blandus*. The genes that modify the shade of gray in these other races, since their effects are similar, are possibly the same genes that modify the shade of gray in *blandus* populations.

TABLE III

MEAN SHADE OF GRAY MICE IN F_2 AND BACKCROSS GENERATIONS OF CROSSES BETWEEN GRAY *blandus* AND MICE OF OTHER RACES, AS SHOWN BY REFLECTION METER READINGS FOR DORSAL RED

Cross	Generation			
	F_2		Backcross	
	Specimens	Dorsal Red	Specimens	Dorsal Red
Gray *blandus* × buff *oreas* (O.B.)	4	12.50	24	16.08 ± 0.41
Gray *blandus* × buff *oreas* (S.L.)	3	13.00	41	15.46 ± 0.32
Gray *blandus* × buff *nebrascensis*	27	16.74 ± 0.39	44	18.41 ± 0.33
Gray *blandus* × buff *gracilis*	1	19.00	37	19.03 ± 0.36
Gray *blandus* × buff *nubiterrae*	5	15.40	12	18.17 ± 0.45
Gray *blandus* × gray *nubiterrae*	8	13.50	......	....

Gray segregants in crosses between gray *blandus* and mice of the subspecies *nubiterrae* are usually more brown in appearance than are gray *blandus* mice. One gray segregant in a cross between *oreas* and gray *blandus* was of this type. This brown effect apparently results from the effects of one or more other color genes. The mode of inheritance of these other genes and their relations to previously described color genes of the deer-mouse have yet to be determined. The brown effect here is not produced by the previously described (Blair, 1947*a*) gene—brown-tipped. A "chocolate" buff was observed in some of the segregants in crosses between *nubiterrae* and *blandus* and between *oreas* and *blandus*. This "chocolate" buff is presumably caused by the same gene or genes that produce the brownish gray observed in those races. Some individuals in eight of the eighteen subspecies represented by field-caught samples are of the brownish gray type. Some of the field-caught buffs, likewise, are "chocolate" buff in appearance. It is evident, therefore, that the gene or genes for this brown character are widely distributed in deer-mouse populations.

SUMMARY AND CONCLUSIONS

This report deals principally with the distribution of the buff and the gray pelage color alleles (G, g) in populations of the deer-mouse (*Peromyscus maniculatus*). Representatives of four subspecies, *nebrascensis, gracilis, nubiterrae,* and *oreas,* were crossed with gray *blandus*. The buff of these other races is dominant over the *blandus* gray. The appearance of the buff hybrids of these crosses and the lack of evident segregation in crosses between buff *blandus* and buff *nebrascensis* and *gracilis* indicate that the same major gene for buff probably is present in all of the races of *maniculatus.*

Buff segregants in the crosses between *blandus* and the other races are extremely variable in shade and in the intensity of yellow-orange pigment in the agouti band of the hairs. This extreme variability of the buffs presumably results from the action of numerous minor modifying genes. Some of the buffs appear to be "chocolate" buff, presumably from the effects of other color genes. Gray segregants are less variable than the buffs, but some of the grays are more brown in appearance than is gray *blandus.* The brownishness of some individuals of both the buffs and grays presumably is caused by the same, as yet undetermined, gene or genes.

All field-caught specimens of deer-mice in the collection of the Laboratory of Vertebrate Biology were examined, and an attempt was made to classify each specimen as buff or gray. Of the 2467 specimens examined, 2089 are classified as buff, and 117 as possibly buff. A total of 177, of which 158 are from the Tularosa Basin, New Mexico, are classified as *blandus*-type gray. Seventy-five specimens are more brown in appearance than is gray *blandus.* These probably are grays modified by other genes.

This preliminary survey of the genetic basis for color variation in the deer-mouse serves principally to suggest possible future lines of attack on the problem of color differentiation in this species. The buff and gray genes, originally studied in *blandus* from New Mexico, are indicated to have wide distribution in the species *maniculatus.* No other members of this allelic series have yet been discovered. Most deer-mice are buff except in the Southwestern deserts, where high frequencies of the gray gene occur in some local populations (Blair, 1947*b*). The frequencies of the buff and gray genes now can be determined in other populations of the species by test matings between representatives of the wild populations and established laboratory strains of the *blandus* color types.

The color differentiation of the dark forest races of the Pacific Northwest and the Eastern forest and of the dark prairie race, *bairdii,* appears to be due in part to the effects of a gene or genes giving a brown tone to the pelage. The mode of inheritance of this character has yet to be determined.

A rich clear buff pelage character predominates in the sandhills of Nebraska. This character has been shown to be a single unit dominant over the dark pelage of such races as *bairdii* and *rubidus.* These alleles seem to be different from the other reported color genes of the deer-mouse, and they need further investigation and description.

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